New Trends in Soil Biology

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Kinetics of water exchange in soil arthropods *

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Summary :

The present study combines gravimetric and tracer techniques using tritiated water (THO). As a rule, three periods of transpiration were detected during which animals were exposed to dehydrating conditions : 1) A short initial period characterized by an increased transpiration rate, 2) a long linear period with a constant water loss rate and 3) an exponential period at the end of desiccation, when the animals had lost all their water reserves. When describing transpiration phenomena it is recommended to give both absolute and relative transpiration rates for the linear period of transpiration, for example in terms of $\mu g\ min^{-1}$, $\mu g\ mm^{-2}\ min^{-1}$, $\mu g\ cm^{-2} h^{-1}\ mmHg^{-1}$ or %/h. The per cent transpiration rates should be related to the linear period of transpiration as well as to the absolute water content m_o in terms of $\triangle$ m [%/h] or k_m. As shown in hygric animals like Collembola, the sorption of THO continued to steady-state or equilibrium within a few hours when exposed to a moist substrate containing tritiated water. Efflux rates were compared at high and low ambient humidity. Lowering of the humidity resulted in a decrease of efflux which implies that changes of cuticle permeability may occur. Data on the absorption or transpiration of tritiated water at high ambient humidity were based on the equation : $\ln | a_t - a_\infty | = \ln | a_o - a_\infty | - k.t$, modified for absorption ($a_o = 0$) and transpiration ($a_\infty = 0$) (a = activity within the animals). Additionally, first data are given on the turnover rates of total water content.

Key words : transpiration, absorption, water exchange, tritiated water, permeability, soil arthropods.

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I. Introduction

Basically, transpiration can be examined from a more physical (ARLIAN & VESELICA, 1979; DEVINE & WHARTON, 1973; MONTHEITH & CAMPELL, 1980; TOOLSON, 1980; WHARTON & DEVINE, 1968) or more ecophysiological point of view (ARLIAN, 1975; CRAWFORD, 1978; EDNEY, 1977; VANNIER, 1983; VERHOEF, 1981; VERHOEF & WITTEVEEN, 1980). Concerning the latter, data on transpiration provide important information on habitat selection of animals and should reveal some of the mechanisms responsible for adaptation of species from aquatic to terrestrial life. Most soil arthropods are highly dependent on a moist environment and soon succumb to desiccation when exposed to the open atmosphere. The threat of dehydration is evidently a serious barrier to terrestrial life.

In the present study I try to develop some principles of water loss, which are based on thermogravimetric analysis at a constant temperature and on flux measurements using tritiated water (THO). Tracer techniques are very useful for indicating independant water fluxes as shown by DEVINE & WHARTON (1973). On the other hand, net water loss rates give more information on the water balance of animals.

II. Materials and methods

Different species or groups of soil arthropods were collected from different microhabitats as litter of beech forests, stone heaps of a quarry and from the water surface. The thermogravimetric analysis was made with a recording Sartorius electrobalance of symmetrical type, kept by a flow-through system at a constant temperature of 22° C. During weighing the specimen was placed in a small cage within a 25 ml glass vial at definite ambient humidity. This technique is classified as still-air weighing, but the animals moved freely within the cage. The efflux of tritiated water from tritium loaded animals could be measured simultaneously by catching the THO molecules while leaving the animal and entering the solution of vials (1 ml pure water or saturated salt solutions). Therefore, a rediffusion of tritiated water into the specimen was neglected. For influx measurements, the animals were exposed to a wet substrate containing tritiated water. Immediately after exposure, they were oxidized by a Packard-sample oxidizer. The sample activity was measured by scintillation technique using Monophase and Instagel as cocktails.

III. Results

1. Water loss rates in soil arthropods

In some cases two components of transpiration were distinguished : a slow and a fast component. The first has to be considered as the main component which is presumably cuticular and continues over long periods. The fast component is characterized by a strong increase of water loss rate over short periods and interrupts the slow component. The rapid water loss can have different causes : excretion, secretion, active regulation of body openings, moulting, movement of special extremities, e.g. pleopods, etc. In most hygric arthropods the slow component dominates and water loss continues at a constant rate. Three periods of transpiration were detected, when animals were exposed to a lowered humidity :

— A short initial period characterized by an increased transpiration rate.

— A long linear period with a constant water loss rate.

— An exponential period at the end of desiccation, when animals had lost all their water reserves.

In hygric soil arthropods the initial period was often finished after a few minutes, but other animals, e.g. some isopods with a relatively thick cuticle, extended this period to about an hour. The linear period of transpiration continued over a long time and the net water efflux remained at a constant rate independant from water content within the animal. It was followed by an exponential period until desiccation, when the animals had lost more than half of their water, i.e. 60-80 %. Most animals died, if the water deficit was more than 30 % of their normal water content. In many cases, e.g. in some species of Collembola, the transpiration rate increased after death (Fig. 3).

2. Influx of tritiated water into body water

When animals were exposed to tritiated water the sorption of THO continued to steady-state or equilibrium between body water and the outer compartment. Fig. 1 demonstrates the sorption of THO in Collembola. Prior to exposure to tritiated water the animals were synchronized in a moist environment in order to establish full hydration. Then they avoided drinking or absorbing by the ventral tube vesicles and the influx of THO happened only by diffusion. The influx followed a typical saturation curve and the body water was equilibrated after about 12 hours. The activity of such tritium loaded animals is termed a_∞. Then the difference between the actual tritium quantity at any time t and at equilibrium $| a_t - a_\infty |$ was plotted as $\ln | a_t - a_\infty |$ against time and the values fitted a straight line. The rate constant k was calculated by regression analysis of $\ln | a_t - a_\infty | = \ln | a_\infty | - k.t$. Therefore the rate constant k can be used as a measure for the decrease of difference in tritium quantity $| a_t - a_\infty |$. In Collembola, as shown in Fig. 1, the rate constant was -0.322 in other terms : -32.2 %/h. Dehydrated animals absorbed water by their ventral tube vesicles immediately after being exposed and the rate constant was increased to -170 %/h for the active absorption of water.

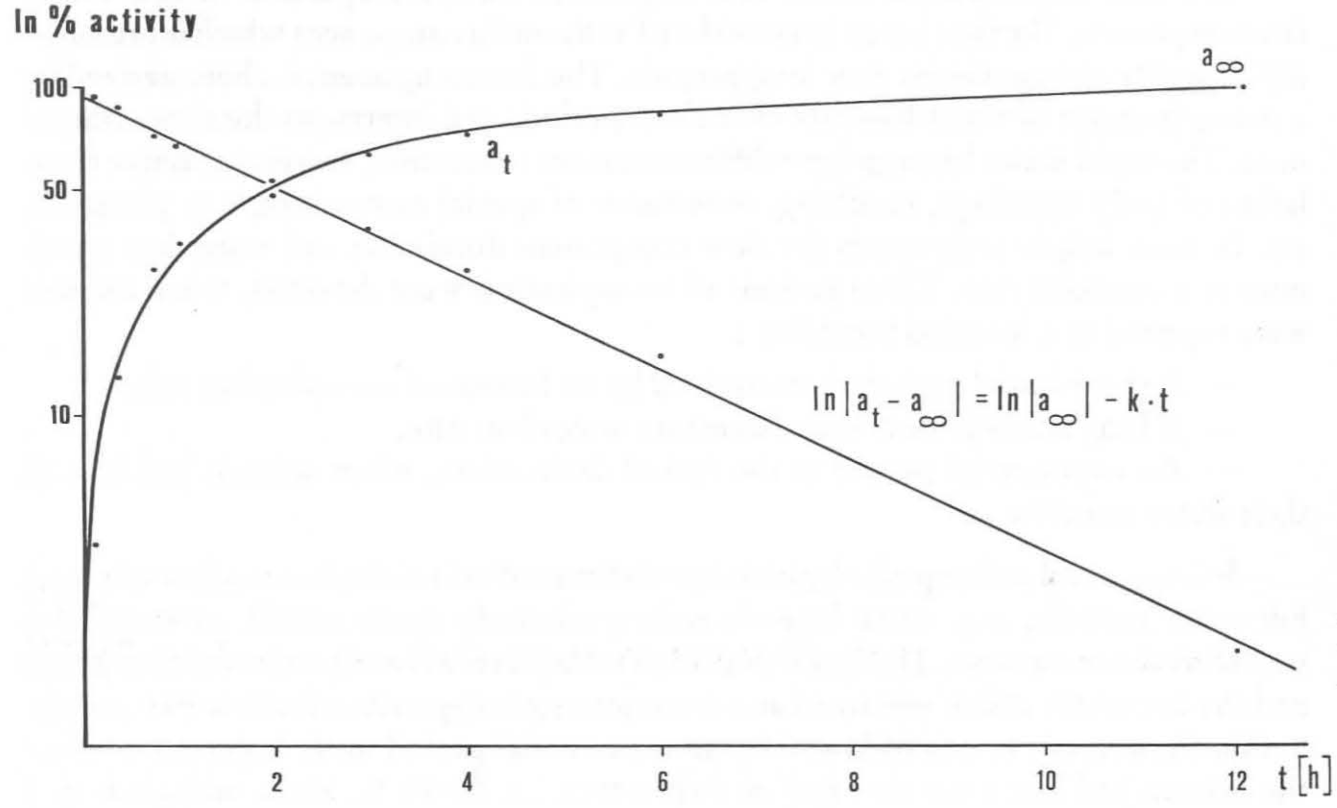

Figure 1 Sorption of tritiated water in Collembola (*Tomocerus* sp.).
Prior to exposure to tritiated water the animals were synchronized in a moist environment in order to establish a full hydration. a_t : activity within the animals at any time t; a_∞ activity within the animals at equilibrium.

3. Efflux of tritiated water at different humidity

A simple method for determining the efflux rates for water is exposing the animals at 0 %r.h. after equilibrium with THO (Fig. 2). The losses of total weight (curve w_t), water content (water mass) (curve m_t) and active water (curve a_t) are compared in a specimen of *Campodea*. It is evident that both, inactive and active water, are cleared nearly at the same rate (k_m = -54.0 %/h and k_a = -53.5 %/h) and that water loss is independent of time and water content during the linear period of transpiration. The initial period was very short and was negligible.

At high ambient humidity the water content remained nearly constant (k_m = -0.2 %/h) as shown in *Tomocerus* (Fig. 3), but THO was cleared at an exponential function. Almost all water molecules leaving the body were replaced by rediffusion of inactive water from the solution of the vial. If data of a_t were plotted as $\ln|a_t|$ against

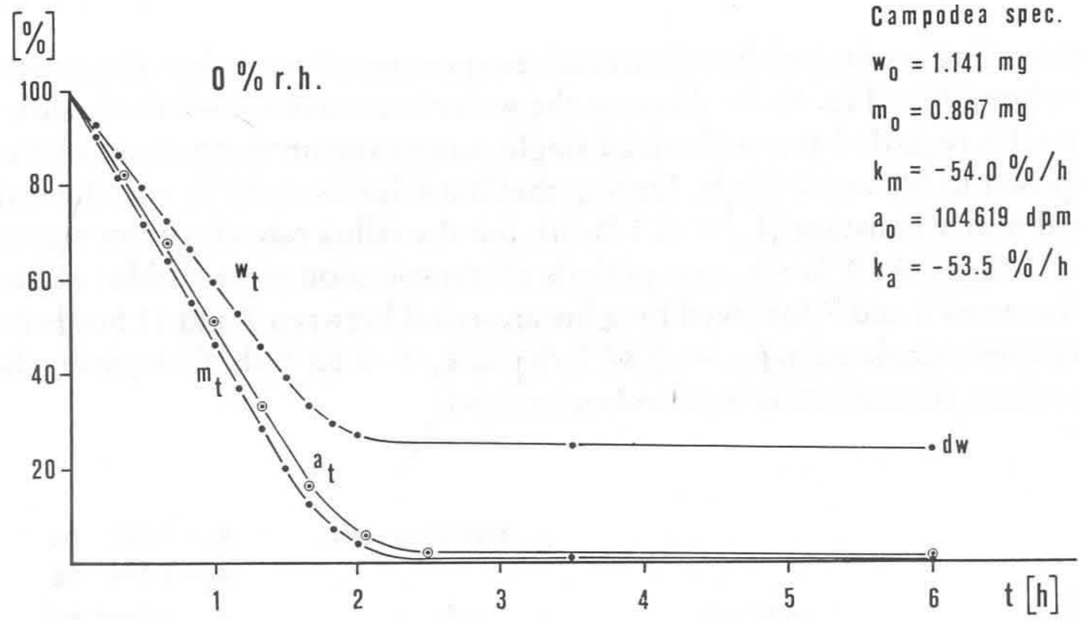

Figure 2 Transpiration for a specimen of *Campodea* sp. (Diplura) at 0 % r.h. and 22° C. Curves of total weight (w_t), water content (m_t) and activity of tritiated water (a_t) within the animal at any time t . w_o, m_o, a_o : fresh weight, water mass and activity at the beginning of exposure. dw : dry weight . k_m and k_a : water loss rate and efflux rate for tritiated water for the linear period of transpiration.

time the values fitted a straight line which is based on the equation $\ln | a_t | = \ln | a_o | - k.t$. « k » could be determined by regression. This rate constant of decrease in radioactivity is also the constant of the efflux of total water. In the example given, the rate amounted to –21.8 %/h. After exposure to 0 %r.h., the water loss increased and all water was extracted within few hours.

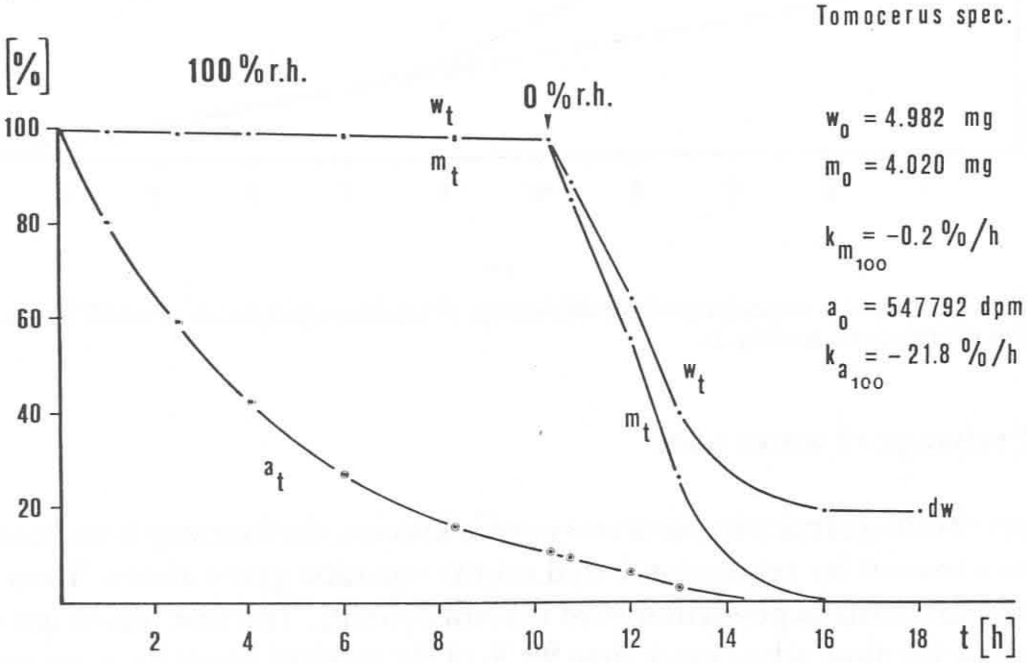

Figure 3 Transpiration for a specimen of *Tomocerus* sp. (Collembola) at 100 and 0 % r.h. and 22° C. For explanations see Fig. 2. k_{m100} and k_{a100} are the water loss rate and the efflux rate for tritiated water at 100 %r.h. The water loss rate increased at 0 %r.h. after the death of the animal.

Interesting results produced successive exposures of mesic dry-air animals to high and low humidity (Fig. 4). In this case the water loss rates are relatively slow and the water pool is regarded as a well mixed single compartment. A specimen of *Neobisium* was exposed to 98 and 0 %r.h. During the first 6 hours at 98 % r.h. the water pool remained nearly constant (k_m = -0.1 %/h), but the efflux rate of tritium was very high (k_a = -2.7 %/h). At 0 % r.h. two periods of transpiration were visible : a short initial period between 6 and 7 followed by a linear period between 7 and 11 hours for which the rates were calculated as k_m = -0.87 %/h and k_a = -0.83 %/h. Comparing the rate of tritium efflux, the reduction was to about a third.

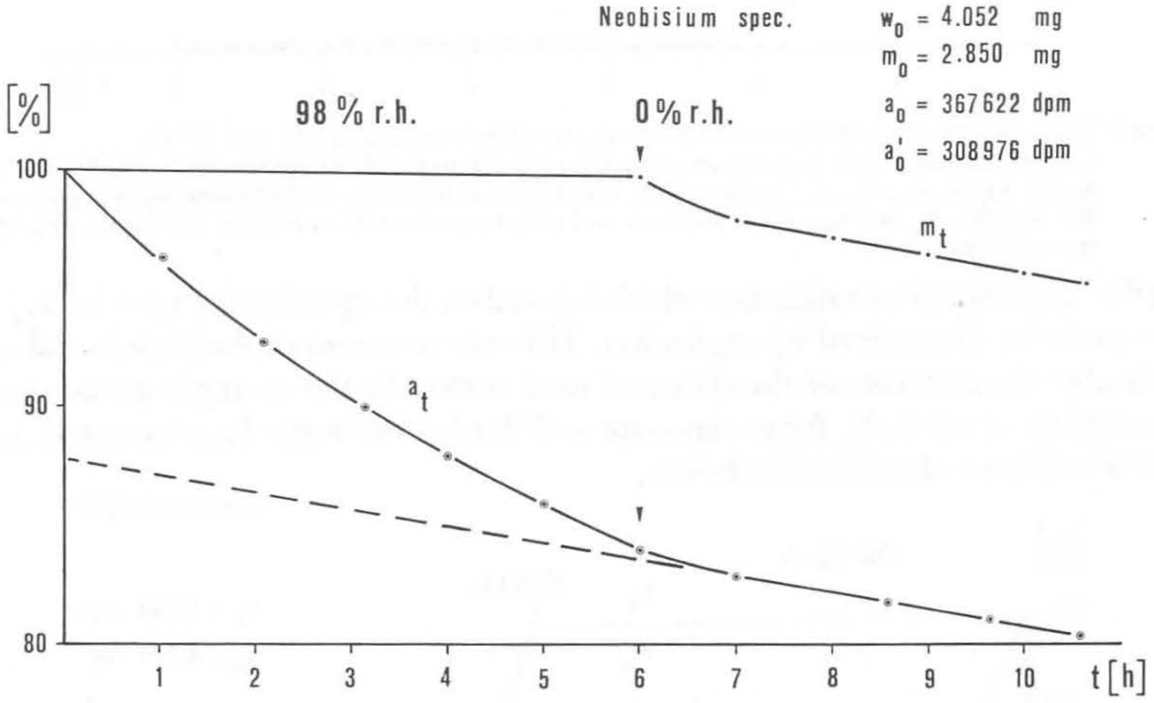

Figure 4 Transpiration for a specimen of *Neobisium* sp. (Pseudoscorpiones) at 98 and 0 % r.h. and 22° C. For explanations see Fig. 2.

4. Exchange of water pool

If the tritium quantity in the water pool is known, the first step is to determine the efflux rate constant by regression based on the equation given above. Then it is very easy to calculate time dependent loss of tritium content. The first results are shown in Table I giving the time when more than 99 % of the original water has been exchanged. Extreme hygric soil arthropods like *Onychiurus*, *Campodea* or *Scutigerella* change their water mass totally within a few hours and mesic dry-air animals like *Lepisma* or *Trigoniophthalmus* need some weeks for it.

TABLE I

Rates of total exchange of water content of different soil arthropods at 22° C.
(More than 99 % of the original water are exchanged).

Group	Genus/Species	r.h.	hours
Chilopoda	*Lithobius* sp.	98	24
	n = 1		
Symphyla	*Scutigerella* sp.	98, 100	6-8
	n = 2		
Pseudoscorpiones	*Neobisium* sp.	98	160
	n = 1		
Diplura	*Campodea* sp.	98, 100	6-8
	n = 2		
Collembola	*Onychiurus* sp.	98, 100	2-4
	n = 2		
	Tomocerus sp.	98, 100	27, 21
	n = 4	98, 100	16, 12
	Orchesella villosa	76, 98, 100	42, 22, 25
	n = 3		
Archaeognatha	*Trigoniophthalmus alternatus*	76, 98	490, 289
	n = 4	76, 98	159, 280
Zygentoma	*Lepisma saccharina*	98, 98	881, 690
	n = 2		

IV. Discussion

The exchange of water between a soil arthropod and the ambient air is well established. The best way to describe net transpiration phenomena seems to compare absolute and relative transpiration rates which are based on gravimetric measurements. Data should be quoted in terms of $\mu g \ min^{-1}$, $\mu g \ mm^{-2} \ min^{-1}$, $\mu g \ cm^{-2} h^{-1} \ mm \ Hg^{-1}$ or %/h. The relative rates, %/h, are an appropriate measure of the change of absolute water content or water mass or, in terms of $\mu g \ cm^{-2} h^{-1} \ mmHg^{-1}$, of the permeability of the integuments. Despite the great complexity of integuments comparative measurements of transpiration rates are valid for ecological purposes and for the compilation of water balance budgets, which was emphasized by EDNEY (1977). As shown in the present study, the main water loss during a dehydration process continues at a constant net rate. Because dry weights are very variable within and between species of soil arthropods, the per cent transpiration rates should not be related to the total weight of animals. It is presumed that soil animals living under natural or comparable conditions balance their water content within an optimal range. Differences between individuals can be considerable, but the average values for groups or populations seem to be relatively constant (EISENBEIS, unpubl.). Recent data on Collembola have revealed that per cent changes in water content are due to changes in dry weight, fluctuating with the feeding rhythm, but the absolute water content stays constant during an instar (VERHOEF, 1981). Therefore it is proposed to give the per cent rates in Δ m [%/h] both for gain and loss of water. Furthermore the rates should be related to the initial absolute water content m_o of normally hydrated animals, kept under natural or comparable conditions. Theses rates are net rates, also termed k_m, and must be distinguished from flux rates of tracers which are termed k_a. Comparing the average water loss rate of an extreme hygric collembolan, *Onychiurus* (k_m = -325.5 % h at 0 % r.h. and 22° C) and the silverfish *Lepisma saccharina* (k_m = -0.37 %/h at 0 % r.h. and 22° C), the rate of the latter is about 900 times lower.

The tracer methods derived from WHARTON & DEVINE (1868) and DEVINE & WHARTON (1973), using tritium water (THO), are very useful to demonstrate counter-current movement of water fluxes at high ambient humidity if no significant changes in water mass occur. A special case was given in Fig. 2 showing a parallel efflux both of tritium and total water at constant rates during the first hour of exposure. Therefore k_m and k_a were related to the water content m_o and to the activity a. When measured at high surrounding humidity, flux data are based on the equation : $\ln | a_t - a_\infty | = \ln | a_o - a_\infty | - k.t$, which can be modified for absorption ($a_o = 0$) : $\ln | a_t - a_\infty | = \ln | a_\infty | - k.t$ or for transpiration ($a_\infty = 0$) : $\ln | a_t | = \ln | a_o | - k.t$. « k » are the rate constants for the efflux or influx of water termed as k_a. Furthermore, it is very easy to calculate the total exchange of water mass. Time rates, as shown in Table I, directly reflect the differences of cuticle permeability. A similar equation was proposed by the above mentioned authors and by ARLIAN & VESELICA (1979) describing the actual water content of dehydrating animals at any time t : $\ln| m_t - m_\infty | = \ln | m_o - m_\infty | - k.t$. This implies that net transpiration rates depend on the actual water content within the animal and that water content curves asymptotically approach an equilibrium value m_∞. But recent measurements of transpiration in a wide range of soil arthropods gave different results. As shown above, net transpiration rates are constant over long periods. It is assumed that — as long as the haemolymph acts as a water store — the integument will be fully hydrated producing a constant efflux of water. Only if water reserves are no longer available, an exponential decrease of water content will occur.

Another field of interest is permeability which can be influenced by temperature and changes in cuticle structure and molecular arrangement (EDNEY, 1977). In *Neobisium* it is evident that water efflux is reduced when the external humidity is lowered. Similar results, based on tracer experiments were received in the thysanuran *Trigoniophtalmus alternatus* (EISENBEIS, 1983). Furthermore, when gravimetric data on transpiration were related to the saturation deficit of the ambient air, the relative rates decreased by lowering the humidity at a constant temperature. This was generally found in very different soil arthropods (EISENBEIS, unpubl.), and changes in cuticle permeability may be one of possible explanations. Dehydrating conditions may also depress O_2 consumption which is considered to be caused by a decrease in permeability, especially if the gas exchange is mediated only by the body surface (ARLIAN, 1975). Consequently, if ambient humidity affects the water exchange and the water loss rate, too, this must be of a high adaptive value in soil arthropods. It is supposed that water exchange at high humidity near saturation and 22° C is about three times more than in dry surroundings.

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Discussion

GHILAROV, M.S. : How significant is metabolic water in water regime regulation of xeric and mesic open air living arthropods ?

EISENBEIS, G. : We calculated the metabolic water production on the base of O_2-consumption of Collembola and we found that metabolic water gain is not significant in respect to changes of water mass due to transpiration. In mites we also found a small amount of metabolic water in the total water mass, as indicated by other workers.

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